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TAXONOMIC RELATIONSHIPS AND PHEROMONE ISOLATION

AMONG WESTERN SPRUCE BUDWORM POPULATIONS

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CANADA/U.S. SPRUCE BUDWORMS PROGRAM - WEST

FINAL REPORT

Taxonomic relationships and pheromone isolation among western spruce budworm populations

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SUMMARY

This study demonstrates that there are two species of Abietoideae-feeding Choristoneura that are sympatric in widespread areas of California, Nevada, and Utah. C. retiniana (Walsingham, 1879) feeds on Abies, has unpigmented larval integument (appearing green in life), weakly pigmented pupal integument, and is dimorphic in color of adults, with two distinct phases in both sexes. Populations of C. carnana (Barnes and Busck, 1920) and C. occidentalis Freeman, 1967, feed on Pseudotsuga when sympatric with retiniana, have heavily pigmented larvae (brick red) and pupae and are monomorphic as adults.

These two species groups are synchronous in flight period where sympatric. Trapping with virgin females and synthetic pheromones indicate a 100% separation in attraction of males, evidently the primary factor in reproductive isolation.

A third species, C. lambertiana (Busck, 1915), which feeds primarily on Pinus, is sympatric with one or the other of the Abietoideae feeders in many areas, and preliminary evidence indicates pheromone chemistry is the isolating mechanism. Three species fly together in a few areas, e.g., retiniana, carnana, and lambertiana subretinana Obraztsov, 1962, in the northern Sierra Nevada; retiniana, occidentalis, and lambertiana ponderosana Obraztsov, 1962, in southwestern Utah.

Morphological variation and pheromone chemistry indicate that carnana and occidentalis are closely related, and it is arbitrary whether these are regarded as species or widespread, polytypic races of a single species. It is suggested that their concepts be retained at the species level, at least until relationships with C. retinana at the northern end of its range are better understood.

OBJECTIVES:

1. To obtain data to define taxonomic and biological relationships between sympatric species of Abietoideae (primarily Abies and Pseudotsuga)-feeding Choristoneura species. Investigations were oriented along four principal lines.

    a) Trapping males in areas of known sympatric associations using caged virgin females and/or synthetic pheromone lures.

    b) Rearing field-collected larvae to discover differential host tree preferences and obtain virgin females.

    c) Obtain egg mass stock from reared females and by caging females collected at blacklight to establish laboratory colonies of selected populations for pheromone chemistry analysis.

    d) Conduct morphological studies of adults, especially micromorphological examinations by SEM, to identify structures useful to identification of taxa.

2. To use survey trapping with synthetic pheromone lures and blacklight to obtain study material, further define geographical distributions and potential host tree associations, and to locate for subsequent study populations in areas where questions of taxonomic identity exist: for Choristoneura occidentalis (Colorado, Utah, and Nevada), C. retiniana (Nevada and southern California), C. carnana (California), and C. lambertiana (all areas visited for the above three species).

3. To obtain data to define taxonomic and biological relationships between sympatric pairs of Abietoideae-feeding and Pinoideae-feeding species.

4. To establish a taxonomic framework based on biological relationships, which will enable predictive qualities for less well known populations, and provide a valid nomenclature for communication purposes.

placed in polyethylene bags with foliage and transported in ice chests. In the laboratory larvae were segregated into small lots in polyethylene bags or plastic rearing boxes and reared on foliage, with daily surveillance to monitor moisture conditions.

Using virgin female-baited traps, a pilot test with californica at Angwin in 1980 demonstrated that emergence of reared females could be delayed up to 10 days by refrigeration (4°C $\pm$ 1.5°) of pupae and/or sexual activity could be delayed by refrigeration of newly emerged adults, without appreciable loss of attractiveness to field males, compared to unrefrigerated individuals reared from the same population (Table 1). Therefore, pupae and/or newly emerged adults were refrigerated to ensure proper timing. In this way we regulated contemporary numbers for mating trials to obtain ova or provide virgin females timed with field emergence of populations to be tested for attractiveness, when these lagged behind larval source areas in seasonal emergence.

2. Trapping males in areas of known sympatric associations.

Virgin females were housed in cages, 3.7 x 3.7 x 3.0 cm in outside dimensions, constructed from cardboard pill boxes and provided with nylon screen windows and a H_2O vial and wick to one side. After transport to the field site in a camp ice chest, each was suspended within a Zoecon Pherocon II® sticky trap. Traps baited either with females or with synthetic pheromone baits were deployed either 20 or 30 m apart, 1.5-2.5 m above the ground. In 1979 traps were set along a line in mixed tree stands, alternating matching and non-matching host trees of the respective Choristoneura lures (e.g., Abies-Pseudotsuga reciprocally with "occidentalis" and "retiniana" baits). There were no statistically significant differences in results with respect to tree species, however, and during 1980-1981 individual trap sites were selected for suspected air movement characteristics rather than tree species.

In 1981 we also used ethylene glycol as a trapping agent, in traps constructed from plastic refrigerator boxes. Experiments at Blodgett Forest were inconclusive as to whether these or sticky traps were more efficient.

Among females of carnana californica deployed at Blodgett, 90% survived more than 7 days in the traps. Early in the season, most lived more than 15 days. Males (n=209) were attracted mostly during the first 7 days during mid-season, but several were trapped between days 8-12, and 2 were attracted between days 17-21 by early season females. No females of C. retiniana were available for early season tests, and those deployed in midseason averaged shorter longevity than carnana, but 70% survived more than 7 days. Only 2 males were attracted after 7 days. These traps were monitored after one night and weekly thereafter, so daily attraction of males was not tabulated.

At other stations, virgin females were deployed for single nights, or traps were left for retrieval after several weeks.

In 1980-1981 virgin females were obtained by larval rearing and deployed for interpopulational cross tests as summarized in Table 2.

RESULTS AND SIGNIFICANCE

Geographical Survey. -- One of the major problems hindering earlier taxonomic assessments was lack of adequate population samples. Available material in collections consisted of geographically scattered samples, often of one or a few specimens, and most had no host plant data (Freeman, 1958; Obraztsov, 1962; Powell, 1964). Later assessments were based on laboratory colonies originating from a few areas of outbreak populations (Freeman, 1967). Therefore, one of the goals of this project was to survey by pheromone and blacklight trapping and by larval collections, as comprehensively as possible, emphasizing known or suspected areas of sympatry among two or more species.

In 1978-1979 preliminary surveys were made along a broad transect across central California to eastern Nevada and in the mountains of southern California. Association of Choristoneura carnana californica (Coast Ranges) and the Sierra Nevada population of this species with Pseudotsuga menziesii was confirmed. Association of C. carnana carnana with P. macrocarpa was postulated on the basis of adult collections and correlated distributions of the moth and plant. Coexistence of 2 Abietoideae-feeding species in the Sierra Nevada was confirmed by pheromone attraction and discovery of larvae of C. retiniana-like populations on Abies concolor.

During 1980 we concentrated field survey on obtaining larvae to produce virgin females for cross-population attraction experiments. Larval collections were made in the Coast Ranges, Trinity, Tehachapi and San Gabriel Mountains (Table 3, Map 1). Later, surveys by virgin female and synthetic pheromone-trapping were carried out in the central Sierra Nevada, along a transect of the eastern Sierra Nevada, northward from Lake Tahoe, in the Adin area of Modoc County, and in eastern Nevada (Table 2). Unfortunately, the "retiniana" and newly developed "subretiniana" baits were ineffective, so that only the virgin female and "occidentalis"-baited trapping produced positive data.

New geographical and host tree information from these surveys included confirmation of C. carnana carnana larval feeding on Pseudotsuga macrocarpa; discovery of carnana californica in northern Mendocino and northern Trinity Counties, feeding on P. menziesii; and coexistence of retiniana and occidentalis in both the Schell Creek and Snake Ranges of eastern Nevada was confirmed.

Early season tests of the "retiniana" bait at Blodgett Forest in 1981 showed a revised formulation, here referred to as "retiniana-C,"to be highly effective, and therefore we expanded survey efforts to obtain attraction data and host tree associations in southern and northern Nevada, northern Arizona, Utah, and repeated the transect along the eastern escarpment of the northern Sierra Nevada. A revised formulation of "subretiniana" bait also proved effective, enabling us to generate geographical data on the pine-feeding complex in several of these areas.

Larval surveys were conducted in 1981 in Napa County and southern California, primarily to obtain livestock for use by Daterman (pheromone assay) and

C. carnana californica feeds on Pseudotsuga menziesii throughout the Coast Range. In northern Trinity County larvae were also found on Abies concolor at 3 sites. At Blue Mountain and Nelson Gap, 14 larvae were taken on Abies (26% of the sample). Most were full grown larvae discovered, conspicuous by their contrasting brick-red color, on young fir saplings that showed little or no evidence of feeding, as though the larvae had recently descended from the mixed Douglas fir-fir canopy. A few, however, were located in feeding shelters on lower limbs of larger Abies. C. retiniana was not found sympatrically in these populations. Mixed populations of the two Choristoneura have been detected a short distance northward, in Siskiyou County.

2. Synthetic pheromone bait trapping:

Circumstantial evidence for the biological isolation of Choristoneura species was provided in two ways by use of synthetic pheromones: a) data on differential attraction of males at sites where two or more species occur sympatrically; and b) attraction at sites selected by differing potential host tree species, generated evidence towards documentation of host specificity.

Three baits were employed (see Techniques). While, the 'occidentalis' lure was effective at the onset of the study, the 'retiniana' baits in 1978-80 and 'subretiniana' bait in 1980 were not. Revised formulations enabled generation of reciprocal data on attractiveness during the 1981 season.

a) Attractiveness in sympatric populations:

Choristoneura retiniana - C. carnana. -- Trapping was carried out at Blodgett Forest, El Dorado Co., during 4 seasons, 1978-1981. There was a 100% separation of males attracted to the baits. The "retiniana-A" bait used in the first 2 seasons was ineffective for this population of C. retiniana (as well as for all others tested), although it was not inert. Several non-target species were attracted including large numbers of tortricids Sparganothis senecionana, Henricus umbrabasana, and an unidentified Cochylinae of another genus. Revised formulations resulted in capture of 19 retiniana in 1980 and 325 in 1981 (Table 4).

Sympatric populations of the same two species displayed equivalent differential preferences along the eastern edge of the Sierra Nevada in Plumas County (Table 5). Traps with "retiniana-C" bait averaged 10.3 males of retiniana, those baited with "occidentalis" lure captured 18.9 males/trap of carnana, while neither attracted reciprocally, at the 3 sites characterized by mixed Abies-Pseudotsuga forests. Bucks Lake, the northernmost station of the transect, at 1590 m is above the limit of Pseudotsuga at that latitude.

Choristoneura retiniana - C. occidentalis. -- Isolation of this pair was tested in 4 mountain ranges of eastern Nevada and central Utah. The "retiniana-B" bait used in 1980 was ineffective, but virgin females used concurrently helped confirm the constancy of differential attraction shown by synthetics in 1981. The single night catches of occidentalis ranged 0.3/trap late in the season (when females predominated at blacklight) at Lehman Creek, to 49/trap

All males captured were attracted by their conspecific females, corroborating synthetic pheromone attraction data at the same localities (Tables 4, 5, 6). At Rush Creek, Modoc Co., neither females nor baits attracted any *Choristoneura*, although larval searches 4 weeks earlier had revealed a low density population there. At Cottonwood Springs, Modoc Co., 4 *retiniana* females caught 33 males, the "retiniana-B" bait and a *carnana californica* female attracted none, while one *retiniana* male was trapped by "occidentalis" bait.

Excluding the Modoc *carnana* null test, 25 females of *carnana* at Blodgett Forest averaged 8.4 males trapped, while 25 *retiniana* females at all locations captured 5.5 males/trap. Low performance at Bucks Lake and Lake Tahoe, 10 males in 6 traps, almost certainly was the result of premature deployment, ahead of the flight period.

Because females were deployed in low numbers and performance of resident females was not matched, no significant comparisons of interpopulational attractiveness within species were generated. In tests with 10 or more females at Blodgett Forest (Table 4), *carnana californica* from Trinity-Siskiyou outcompeted those from Lake-Mendocino (12.3 to 5.6 males/trap), while Lake Co. *californica* and *carnana carnana* females attracted comparable numbers. The Trinity-Siskiyou area is much more distant by straightline measure from Blodgett, than is Lake County, but Trinity is nearer by *Pseudotsuga* forest connection (Map 2), and the performance of its females at Blodgett was comparable to resident females at Angwin, Napa Co. (14.7 males/trap, Table 1), where the *californica* population is more dense according to our larval surveys and blacklight collections.

The greatest distances separating populations used in cross attraction tests were San Gabriel Mts. *carnana carnana* to Blodgett Forest (580 airline km), and Modoc Co. *retiniana* to the Schell Creek and Snake Ranges, Nevada (565-595 airline km). The latter's single trap-night catches of 10 and 14 *retiniana* suggested that these distances have no appreciable effect on pheromone relationships.

4. Flight periods.

The relative seasonal activity of sympatric species has been monitored at only two sites among the populations discussed here. At Blodgett Forest flight periods of *retiniana* and *carnana* were sampled in 1967, 1980 and 1981. Activity of *retiniana* and *subretiniana* was documented by light trap collections at the Warner Mountains in 1922 by A. W. Lindsey (Powell, 1964: 176, 183) and at Tahoe City during 1975-1981 by N. Westerland.

In each pair, the spans of seasonal activity and the peak in abundance are approximately the same (e.g., Graphs 1, 2). Our data at Blodgett originated from continuous trapping of males by synthetic pheromones and virgin females from distant populations, supplemented by weekly light trap collections. They are incomplete because sampling in 1981 was initiated after the flight period had begun and in 1980 data are not fully comparable between species because the "retiniana-B" bait was only weakly effective and virgin

are usually brown but are variable in the northwestern portion of the geographic distribution. C. lambertiana have orange to reddish-brown scales. Hindwing color is sometimes helpful in identifying sympatric species and recognizing geographic variation within a species.

3. Polymorphism in wing color:

C. retiniana expresses genetic polymorphism in forewing pattern. Populations consist of two phenotypes in both sexes, one with orange forewings patterned by transverse rows of black flecks or lines ("mottled"), which is the typical form originally described by Walsingham and named spaldingiana by Obraztsov. A completely distinct morph has tan forewings ("buff"), marked at most by indistinct, rust colored, longitudinal streaks. This form was named lindseyana by Obraztsov, who believed it was another species. C. retiniana populations at the northern edge of the range, in northernmost California and southern Oregon are more variable in wing pattern, but the two forms remain distinct.

The proportions of these morphs are geographically variable, and reach 1.6:100 in the eastern Nevada populations, with only one mottled individual in our samples (n = 60).

C. carnana, by contrast, is monomorphic. Although more variable in pattern in the Coast Ranges (carnana californica), there is no indication of genetic polymorphism in color pattern. Some aspects of sexual dimorphism in wing pattern are displayed, but the sex-linked color morph polymorphism known in females of fumiferana and occidentalis are not recognizable in carnana.

C. occidentalis and C. lambertiana populations in the areas discussed here also are variable in phenotype but do not exhibit polymorphism parallel to that of C. retiniana.

4. Wing Length: C. carnana and C. occidentalis tend to have the longest wings. C. retiniana tends to have the shortest wings.

5. Wing Length-to-Width Ratio: C. carnana and C. occidentalis wings tend to be proportionately broadest: C. retiniana has narrower wings, also a more variable character in northern populations; and C. lambertiana wings tend to be proportionately narrowest.

6. Genitalia Characters: Males of C. occidentalis and C. carnana usually have a proportionately smaller aedeagus tip and broader uncus than those of the other species. The aedeagus tip is longest and uncus narrowest in C. lambertiana. Female signa average slightly larger among C. lambertiana.

7. Tarsal Spines: There are statistically significant differences among numbers and variances of basitarsal spines on the mid- and hindlegs when popula- tions of budworm adults are compared. This seems to be of greater magnitude when expressed as geographic variation within species than it is as a consis- tent diagnostic difference between species.

which has reddish larvae that are easily distinguished from the green budworms in that population, while miscellaneous other associates (10 species) made up only 1.5% of the samples. In sparse populations, however, there may be widely varying proportions of Choristoneura and microlepidoptera caterpillars of other species. Some examples from our 1979-1980 collections are as follows:

Pseudotsuga in Napa and Lake counties, where Choristoneura carnana californica is moderately populous (6-10 larvae/search hr), yielded 74 and 85% Choristoneura, respectively, among microlepidoptera reared.

In Sonoma County, however, all larvae reared from 6 hrs search in 1980 in the vicinity of a 1967 light trap collection of adult C. carnana californica proved to be other species, representing 3 genera of tortricids (Griselda radicana, Acleris gloverana, Archips argyrospilus).

Pseudotsuga at Blodgett Forest, El Dorado County, with sparse larval density (1-2 larvae/search hr) produced 57% Choristoneura.

Abies consistently yielded low proportions of C. retiniana, except at Tehachapi where there is a relatively dense population, and the community of associated species on Abies is more diverse than on Pseudotsuga (Table 7).

In the Tahoe City area several collections produced an aggregate of 34.5% C. retiniana, along with 6 other species; while lots from 3 sites in the Manzanita Mtn. area, Modoc County, in June and July, 1980, yielded 27% retiniana, 33% Griselda radicana, and 40% among 5 other species.

At Blodgett Forest, only 6.6% of moths emerging from our Abies concolor samples during the two seasons were C. retiniana. Similarly, in a single collection at Hockaday Springs, Siskiyou Co., only one of 15 green larvae feeding in webbed buds proved to be retiniana. The remainder included 3 genera of Tortricine moths, Argyrotaenia dorsalana, Clepsis persicana forbesi, Sparganothis senecionana, with the last, a general feeder, most common.

Our data indicate that associated species often make up an appreciable proportion of the budworm community, the composition of which can be predicted neither from place to place nor season to season. Moreover, our observations on discrimination of living early instar larvae suggest that field inventories of immature instar larvae for purposes of monitoring and/or predicting phenology or other lifetable characteristics may not be reliable in sparse populations.

2. Pheromone trap catches. -- A large number of non-target moths, representing a broad taxonomic diversity, were trapped using synthetic pheromone baits, particularly during 1978-1979. Virgin females, by contrast, attracted no moths other than conspecific males. It seems obvious that the natural product is specifically evolved so as to exclude other species, while synthetic pheromones thus far developed offer only a crude approximation emphasizing major compounds of the attraction and few of the inhibitors.

CONCLUSIONS

This work demonstrates that there are two species of Abietoideae-feeding Choristoneura that are sympatric in widespread areas of California, Nevada and Utah. A third species, which is primarily restricted in larval feeding to Pinoideae, is sympatric with one or both of the Abietoideae series in some populations, but it was not emphasized in this study.

Choristoneura retiniana (Walsingham, 1879) feeds on Abies, has unpigmented larval integument (appearing green in life), weakly pigmented pupal integument, and dimorphic color phases in the adult. Its sex pheromone is a E-11 tetradecenyl acetate based compound. This species occurs in the mountains of California, Great Basin ranges, and Wasatch Range of north central Utah (Map 3). Synonyms: lindseyana Obraztsov, 1962; spaldingiana Obraztsov, 1962; viridis Freeman, 1967.

Choristoneura carnana (Barnes and Busck, 1920) feeds on Pseudotsuga, has heavily pigmented larval integument (appearing mottled, brick red in life), heavily pigmented pupal integument, and is monomorphic in adult color. Populations in southern California (typical carnana carnana) feed on P. macrocarpa, those in the Sierra Nevada and north Coast Ranges of California (carnana californica Powell, 1964) feed on P. menziesii. The sex pheromone is a E-11 tetradecenal based compound. C. carnana occurs in the San Gabriel Mountains, central Sierra Nevada, southern Cascade Range, and north Coast Ranges of California (Map 4).

Choristoneura occidentalis Freeman, 1967, feeds on various Abietoideae, and in the literature is reported in the northwestern states to have more variable pigmentation of larvae, pupae and adults than the two preceding species show in California. In the areas encompassed by this study, occidentalis was associated with Abies lasiocarpa in northern Nevada, with mixed stands of Abies and Pseudotsuga in eastern Nevada and northern Arizona, and with mixed Abies-Picea-Pseudotsuga forests in Utah, but no direct evidence on host tree preference was produced. The pheromone is a E-11 tetradecenal compound, evidently very similar to that of carnana.

Choristoneura lambertiana (Busck, 1915) feeds on Pinus, has heavily pigmented larval and pupal integument, and is monomorphic in adult color in any given population. The adult phenotype, however, is markedly polytypic, and named subspecies are assigned to the pine-feeding series in the belief they all represent one species (Map 5):

C. l. lambertiana is known only from south central Oregon and adjacent Siskiyou County, CA, where it is known to feed on Pinus lambertiana.

C. l. subretiniana Obraztsov, 1962, occurs in southern California, along the crest and east escarpment of the Sierra Nevada and in the Warner Mountains of northeastern California, associated with its primary host, Pinus contorta.

C. l. ponderosana Obraztsov, 1962, is distributed on the east slope of the Rocky Mountains in Colorado and in western Nebraska, with populations of

Sex pheromone chemistry, however, appears to be the primary reproductive isolation mechanism in all sympatric populations discussed here. While inter-species matings resulting in fertile F_1, families may be obtained in the laboratory among various Choristoneura (Volney, Liebhold, pers. correspondence), none of the sympatric population pairs discussed here have been tested. Cross-population tests with virgin females showed 100%, and sympatric synthetic pheromone tests showed a greater than 99%, separation of males attracted in the field. There is no evidence from our larval collections or from adult specimens that hybridization occurs in natural populations in the areas examined in this study.

Nomenclature. -- It is obvious that three budworm groups perform as reproductively isolated species in the southwestern U.S., and the oldest names applied to them are retiniana (1879), lambertiana (1915), and carnana (1920). In the northwestern U.S., Abietoideae-feeding populations show more variability in adult and larval phenotype and in host preference, and these are assigned the name occidentalis (1967). By pheromone chemistry and both adult and larval characteristics occidentalis appears to be more closely related to carnana than to retiniana. Therefore it is arbitrary whether Choristoneura carnana (including its northern populations, californica), and occidentalis are considered to be separate species or geographic races of a single widespread, polytypic species. In the interest of stability, we recommend continuing to regard them as species, at least until we have better understanding of relationships between retiniana and occidentalis.

Thus the nomenclature previously outlined (Powell, 1980) can be used, except that spaldingiana Obraztsov, 1962, will be a synonym of retiniana. Treatment of spaldingiana as a subspecies (Great Basin ranges and Sierra Nevada) does not seem advisable in view of discordant geographic variation in variability of several characters.

considerable insight into Choristoneura biology, techniques, and forest entomology practices generally, throughout the study. Their work in northern California prior to, and in Oregon during early phases of the CANUSA-West project, was instrumental in development of several aspects of our study.

N. Westerland, 635 Twin Peaks Dr., Tahoe City, California, carried out continuous blacklight trapping during 1974-1981, providing flight period and relative abundance data for Choristoneura retiniana and subretiniana. He and Florence Westerland cooperated by monitoring pheromone traps and providing us with hospitality many times during the 1979-1981 field seasons.

MANUSCRIPTS PLANNED

Powell and De Benedictis. Biological and taxonomic relationships of conifer-feeding *Choristoneura* in the southwestern United States.

De Benedictis and Powell. Phenetic comparisons among populations of conifer-feeding *Choristoneura* in the western United States.

Daterman et al. Effectiveness of synthetic pheromone lures for three species of *Choristoneura* in Oregon and California.

Powell and De Benedictis. Techniques employing virgin female-baited traps in biosystematic studies of closely related moths.

De Benedictis and Powell (and Daterman?). Non-target Lepidoptera attracted to synthetic lures designed for three species of *Choristoneura* (Tortricidae).

Table 1. Test of attractiveness by females of <u>Choristoneura carnana californica</u> following refrigeration
(Larvae collected 21 May 1980, traps deployed 17-20 June, 1980
1 km SE and 3 km NE Angwin, Napa Co., CA, JAP 80E42)

Female #	Days pupa refrigerated	Days moth refrigerated	Males attracted
1	--	14	2
2	--	11	4
3	--	8	24
4	--	7	24
5	--	7	15
6	--	6	25
7	7	6	18
8	7	5	12
9	10	2	3
10	10	0	20

Table 2. Source and test site data for cross-population attractiveness experiments with virgin females

Species	Larval Source	Deployed at	(Trap Numbers)
1980:			
carnana carnana	San Gabriel Mts.	Blodgett	(3)
carnana californica	Lake Co.	Blodgett	(10)
"	Mendocino Co.	Blodgett	(2)
"	Trinity Co.	Blodgett	(11)
"	"	Modoc Co.	(2)
retiniana	Modoc Co.	Blodgett	(1)
"	"	Schell Cr. Range	(1)
"	"	Snake Range	(1)
retiniana	McCloud Summit, Sisk. Co.	Blodgett	(1)
retiniana	Tehachapi Mt.	Blodgett	(10)
"	"	Modoc Co.	(7)
1981:			
retiniana	Tehachapi Mt.	Bucks Lk., Plumas Co.	(2)
"	"	Sulphur Cr., Plumas Co.	(1)
"	"	Tahoe City	(4)

Table 3. Hostplant associations in natural populations of *Choristoneura* in California, based on adults reared from field collected larvae

Species	JAP Lot No.	Locality	Hostplant
C. carnana carnana	80F29	5 km NE Mt. Baldy, S. Berdo Co.	*Pseudotsuga macrocarpa*
"	81F106	"	"
"	80F38	6 km S Crystal Lk., Los Angeles Co.	"
C. carnana "Sierran population"	79F26, F33	Blodgett Forest, El Dorado Co.	*Pseudotsuga menziesii*
"	80F108	"	"
"	81F116	"	"
"	79F38	"	*Abies concolor*
C. carnana californica	79E42, E43, E74	3 km NE Angwin, Napa Co.	*Pseudotsuga menziesii*
"	80E36	"	"
"	79E59	1.5 km W Angwin	"
"	80E31	"	"
"	80E42	1.5 km SE Angwin	"
"	81E38	"	"
"	80F7	Mt. St. Helena, Napa Co.	"
"	79E80	1.5 km NE Cobb, Lake Co.	"
"	80E49, F12	"	"
"	80E55	2.5 km W Branscomb, Mendocino Co.	"
"	80F43	Blue Mtn., Trinity Co.	"
"	80F47	"	*Abies concolor*
"	80F49	Nelson Cr. Gap, Trinity Co.	*Pseudotsuga menziesii*
"	80F52	"	*Abies concolor*
"	80F53	Scott Mtn., Trinity Co.	*Pseudotsuga menziesii*

Table 3. cont.

Species	JAP Lot No.	Locality	Hostplant
C. carnana californica	80F58	Shadow Creek, Siskiyou Co.	*Pseudotsuga menziesii*
"	80F70	6 km SW Etna, Sisk. Co.	"
"	80F73	" "	*Abies concolor*
"	80F76	Willow Cr., Siskiyou Co.	*Pseudotsuga menziesii*
C. retiniana	80F64	Hockaday Spr., Sisk. Co.	*Abies concolor*
"	80F93	McCloud Summit, Sisk. Co.	*Abies concolor*
"	80F98	Rush Creek, Modoc Co.	"
"	80F105, G19	Cottonwood Spr., Modoc Co.	"
"	79G5	Ward Cr., 3 km SW Tahoe City, Placer Co.	*Abies* (*magnifica* ?)
"	79G10	6 km S Tahoe City, Placer Co.	"
"	80G17	"	"
"	79F30	Blodgett Forest, El Dorado Co.	*Abies concolor*
"	80F25	Tehachapi Mt., Kern Co.	*Abies concolor*
"	81F101, 104	"	"
"	81F115	E. Slope Mt. Pinos, Kern Co.	"
"	81F113	Fir Ridge, Mt. pinos, Ventura Co.	"
"	81F108	Blue Ridge Summit, Los Angeles Co.	"
C. lambertiana subretiniana	80G13	Sagehen Cr., Nevada Co.	*Pinus contorta*
"	80G15	Donner Camp, Nevada Co.	"
"	79G1	Donner Summit, Nevada Co.	? *Picea*
"	80G18	6 km S. Tahoe City, Placer Co.	*Abies magnifica*?

Table 4. Choristoneura males taken in traps baited with synthetic pheromones and virgin females during 4 seasons in the Blodgett Forest area, El Dorado Co., CA

Bait	(No. traps)	No. of male moths trapped: C. retiniana	C. carnana	Avg./trap
1978:				
"retiniana-A"	(18)	0	0	-
"occidentalis"	(18)	0	70	3.9
1979:				
"retiniana-A"	(11)	0	0	-
"occidentalis"	(12)	0	201	16.7
1980:				
"retiniana-B"	(6)	19	0	6.3
C. retiniana Tehachapi	(10)	60	0	6.0
C. retiniana Modoc Co.	(1)	1	0	1.0
C. retiniana Siskiyou Co.	(1)	1	0	1.0
"occidentalis"	(6)	0	66	11.0
C. carnana carnana San Gabriel Mts.	(3)	0	19	6.3
C. c. californica Lake - Mendocino	(12)	0	67	5.6
C. c. californica Trinity - Siskiyou	(10)	0	123	12.3
1981:				
"retiniana-C"	(21)	325	0	15.5
"occidentalis"	(20)	0	101	5.0
Total		406	647	

Table 5. Choristoneura males taken in traps baited with synthetic pheromones and virgin females during a 4-week period, July-August, 1981, in Plumas County, CA

Bait	(No. traps)	C. retiniana	C. carnana	C. l. subretiniana	Avg./trap
		No. of male moths attracted			
Bucks Lake:					
"retiniana-C"	(2)	46	0	0	23
retiniana / Tehachapi	(2)	2	0	0	1
"occidentalis"	(2)	0	0	0	
"subretiniana"	(2)	0	0	61	30.5
Big Creek Rd.:					
"retiniana-C"	(3)	20	0	0	6.3
"occidentalis"	(3)	0	57	0	19
"subretiniana"	(3)	1	0	0	0.3
Sulphur Creek:					
"retiniana-C"	(2)	20	0	0	10
retiniana / Tehachapi	(1)	9	0	0	9
"occidentalis"	(3)	0	61	0	20.3
"subretiniana"	(3)	0	0	1	0.3
Gold Lake Rd.:					
"retiniana-C"	(3)	43	0	0	14.3
"occidentalis"	(3)	0	52	0	17.3
"subretiniana"	(3)	0	0	0	

Table 6. Choristoneura males taken in traps baited with synthetic pheromones or virgin females during single night tests in Nevada and Utah, in August 1980 and July 1981.

Bait	(No.traps)	No. of male moths attracted			
		C. retiniana	C. occidentalis	C. l. ponderosana	Avg./trap
Timber Cr., NV:					
"retiniana-B"	(2)	0	1	0	0.5
retiniana Modoc Co.	(1)	10	0	0	10
"occidentalis"	(2)	0	98	0	49
Wheeler Peak Rd., NV:					
"retiniana-B"	(2)	0	0	0	-
retiniana Modoc Co.	(1)	14	0	0	14
"occidentalis"	(2)	0	80	0	40
Lehman Cr., NV:					
"retiniana-C"	(3)	24	0	0	8
"occidentalis"	(3)	0	1	0	0.3
"subretiniana"	(3)	0	0	0	-
Willis Cr.-Duck Cr., UT:					
"retiniana-C"	(4)	42	0	0	10.5
"occidentalis"	(4)	0	7	0	1.75
"subretiniana"	(4)	0	0	17	4.25
Mt. Timpanogos, UT:					
"retiniana-C"	(5)	33	0	0	6.6
"occidentalis"	(5)	0	23	0	4.6

Table 7. Microlepidoptera species other than *Choristoneura* reared from budworm collections in California during 1979-1981
(*) designates species presumed to be incidental associates from other plants

Taxa	Host tree	Lot Nos.	(Total Lots)
PYRALIDAE, PHYCITINAE:			
Dioryctria species	*Pseudotsuga menziesii*	79E56 80F8, F17, F48, F77	(5)
Dioryctria species	*P. macrocarpa*	80F30	(1)
Dioryctria species	*Abies concolor*	80F26, F54 81F101	(3)
Dioryctria species	*Pinus contorta*	79G16	(1)
TORTRICIDAE, OLETHREUTINAE:			
(*)*Epinotia emarginana* (Wlsm.)	*Pseudotsuga menziesii*	79E45	(1)
E. trossulana (Wlsm.)	*Abies magnifica* (?)	79G10 80F55, F65, G17	(4)
E. meritana Heinr.	*A. concolor*	81F104	(1)
Griselda radicana Heinr.	*Pseudotsuga menziesii*	79E60, E81, F3, F8, F27, F37	(6)
"	*A. magnifica* (?)	79G13	(1)
"	*Abies concolor*	80F46, F54, F77, F87 F100, F103, F110, G19 79F29, F40	(10)
Zeiraphera ?pacifica Free.	*A. concolor*	80G21	(1)
TORTRICIDAE, TORTRICINAE:			
Acleris gloverana (Wlsm.)	*Pseudotsuga menziesii*	79F3, F12 80F71	(3)
"	*Abies concolor*	79F40 80F93, F95, G1, G19 81F118	(6)
	A. magnifica (?)	79G3, G10, G13	(3)

Table 7. cont.

Taxa	Host tree	Lot Nos.	(Total Lots)
Archips argyrospilus (Wlk.)	Pseudotsuga menziesii	79E44, E61, F15, G15 80E34, E50, F3, F18 F47, F59, F77	(11)
Argyrotaenia dorsalana (Dyar)	Abies magnifica (?)	79G15	(1)
"	A. concolor	80F66	(1)
A. provana (Kearfott)	Pseudotsuga menziesii	79F34 80F44	(2)
"	Abies concolor	80F94, G19	(2)
A. lautana Powell	Pseudotsuga macrocarpa	80F29	(1)
A. citrana (Fernald)	P. menziesii	80E48	(1)
Choristoneura rosaceana (Harris)	P. menziesii	80E31	(1)
lepsis persicana forbesi Obr.	Abies concolor	80F66, F105	(2)
Amorbia cuneana (Wlsm.)	Pseudotsuga menziesii	80E57	(1)
Sparganothis senecionana (Wlsm.)	Abies magnifica (?)	79G9, G10	(2)
"	A. concolor	80F66	(1)
"	Pseudotsuga menziesii	80F68	(1)
GELECHIIDAE:			
(*)Adrasteia sedulitella (Bsk.)	P. menziesii	79E55	(1)
Coleotechnites "coniferella complex A"	P. menziesii	79F37 80E36, E53, E56, F80	(5)
Coleotechnites "coniferella complex B"	Abies concolor	79F28, F39 80F64, F74, F88, F91 F99, F105, F112 81F108, F109, F115, F117	(13)
"	A. magnifica (?)	79G8, G14, 80G17	(3)

Table 7. cont.

Taxa	Host tree	Lot Nos.	(Total Lots)
Coleotechnites "Heteromeles complex"	*Pseudotsuga menziesii*	80E42, F21, F82	(3)
"	*P. macrocarpa*	80F35, F40 81F107	(3)
Coleotechnites (?) (tan species)	*Abies concolor*	81F108, F113	(2)
Chionodes "tessa complex"	*A. concolor*	80F26, F90, F114 81F101	(4)
"	*Pseudotsuga menziesii*	80F48	(1)
Chionodes "sabinianae complex"	*P. menziesii*	80E39, E44	(2)
"	*Abies concolor*	80F26	(1)
Undetermined genus (white)	*Pseudotsuga macrocarpa*	80F33 81F106	(2)
BLASTOBASIDAE:			
Holcocera species	*Abies concolor*	79F31	(1)
PLUTELLIDAE:			
Zelleria haimbachi (Bsk.)	*Pinus jeffreyi*	79G19	(1)
"	*Pseudotsuga menziesii*	80F59	(1)
"	*P. macrocarpa*	81F107	(1)
(*)*Harpipteryx dentiferella* (Wlsm)	*Abies magnifica* (?)	79G11	(1)
(*)*Abebaea cervella* (Wlsm.)	*Pseudotsuga menziesii*	80F59	(1)
(*)*Plutella ?dammersi* Bsk.	*Abies concolor*	81F113	(1)

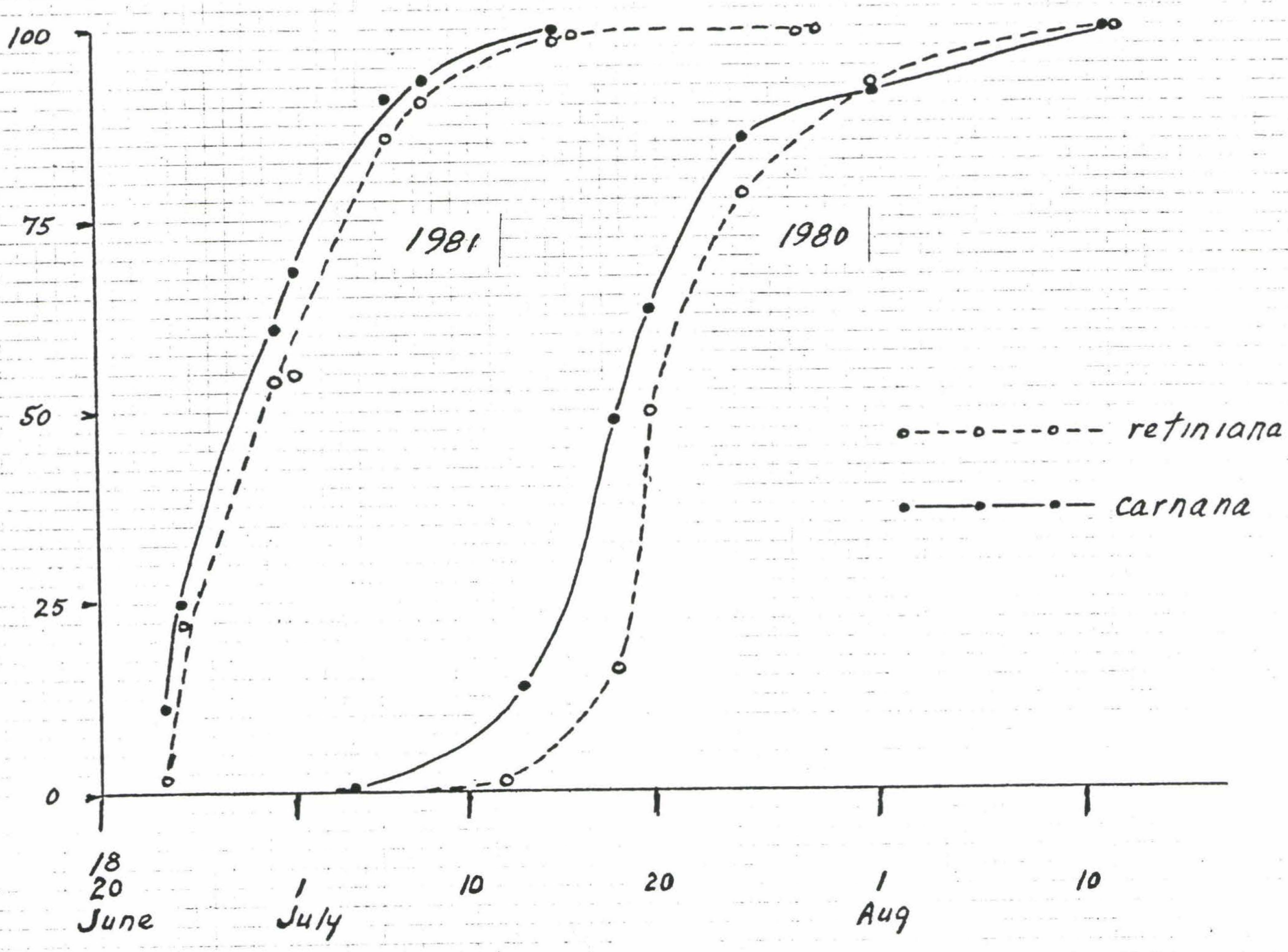


Fig. 1. Cumulative percent activity of Choristoneura retiniana and C. carnana during two seasons at Blodgett Forest, El Dorado Co., CA, as indicated by continuous pheromone trap and weekly blacklight trap samples. In both years the mean of total catch for carnana preceded that of retiniana by 2-3 days, but the apparent lag in retiniana emergence in 1980 is believed to be partly artifactual because virgin females of retiniana were not available until 14 days after sampling began. The 1981 data do not reflect a sigmoid curve because flight had commenced prior to initiation of sampling. retiniana: n = 140 (1980), 355 (1981); carnana: n = 338 (1980), 130 (1981).

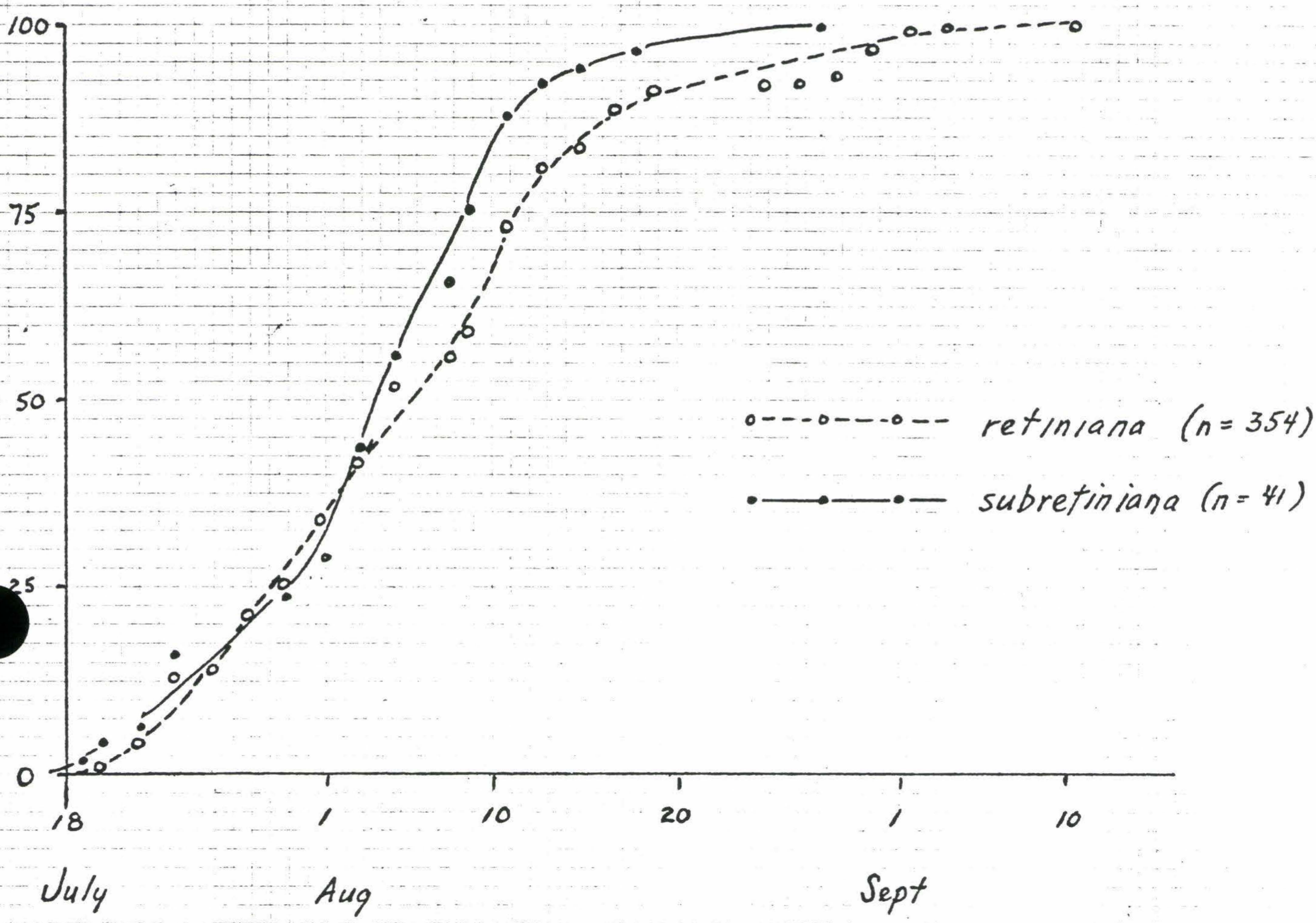
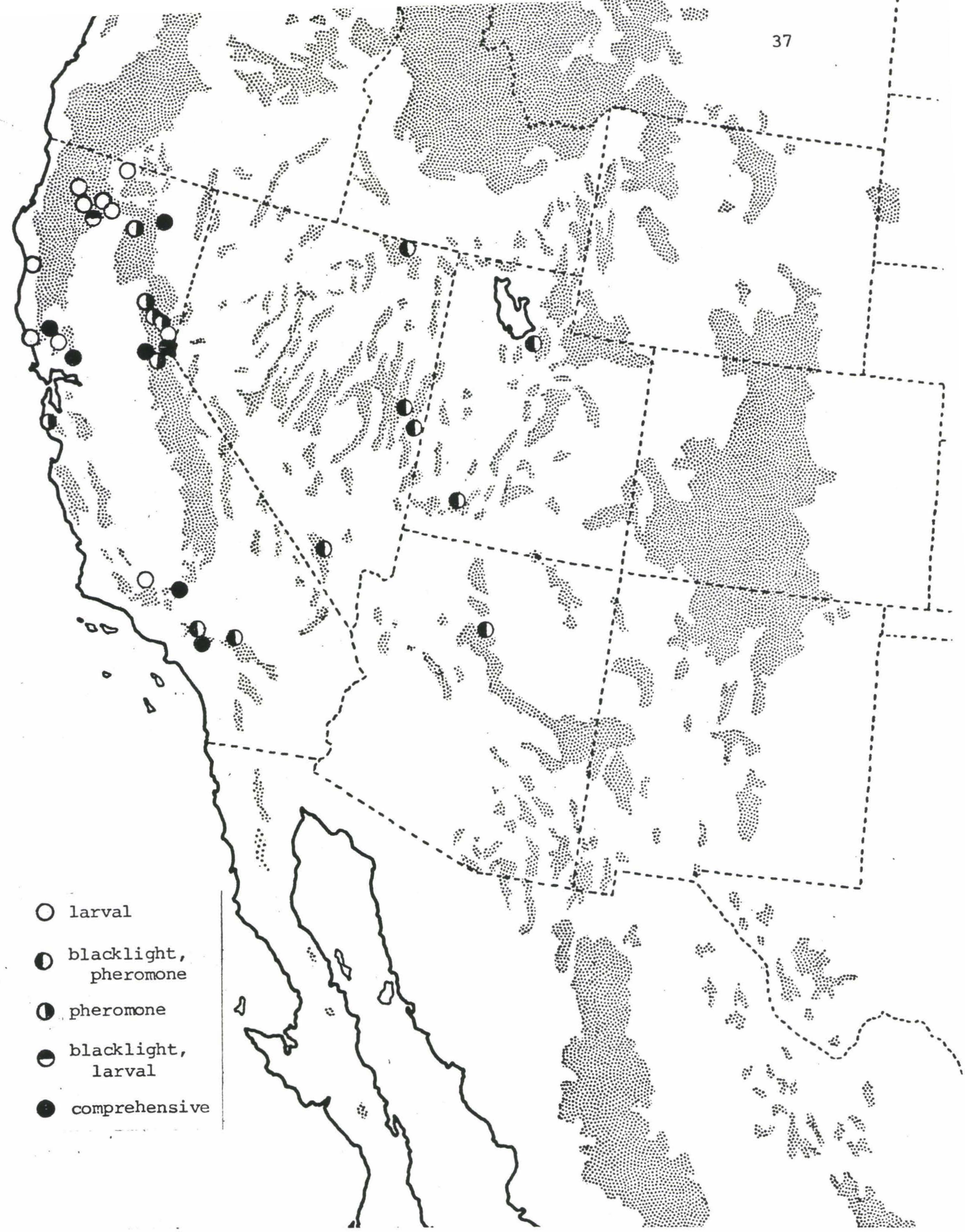
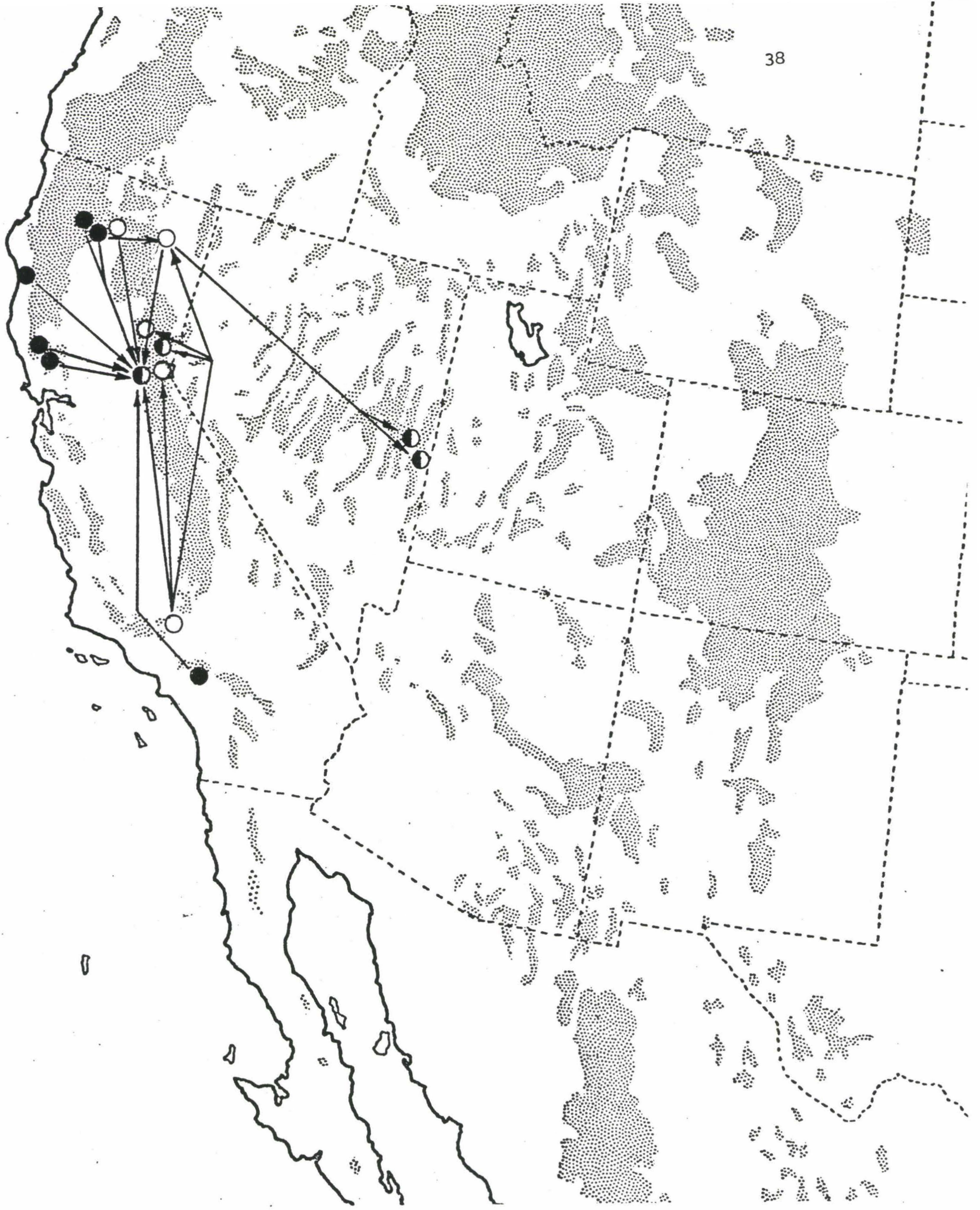


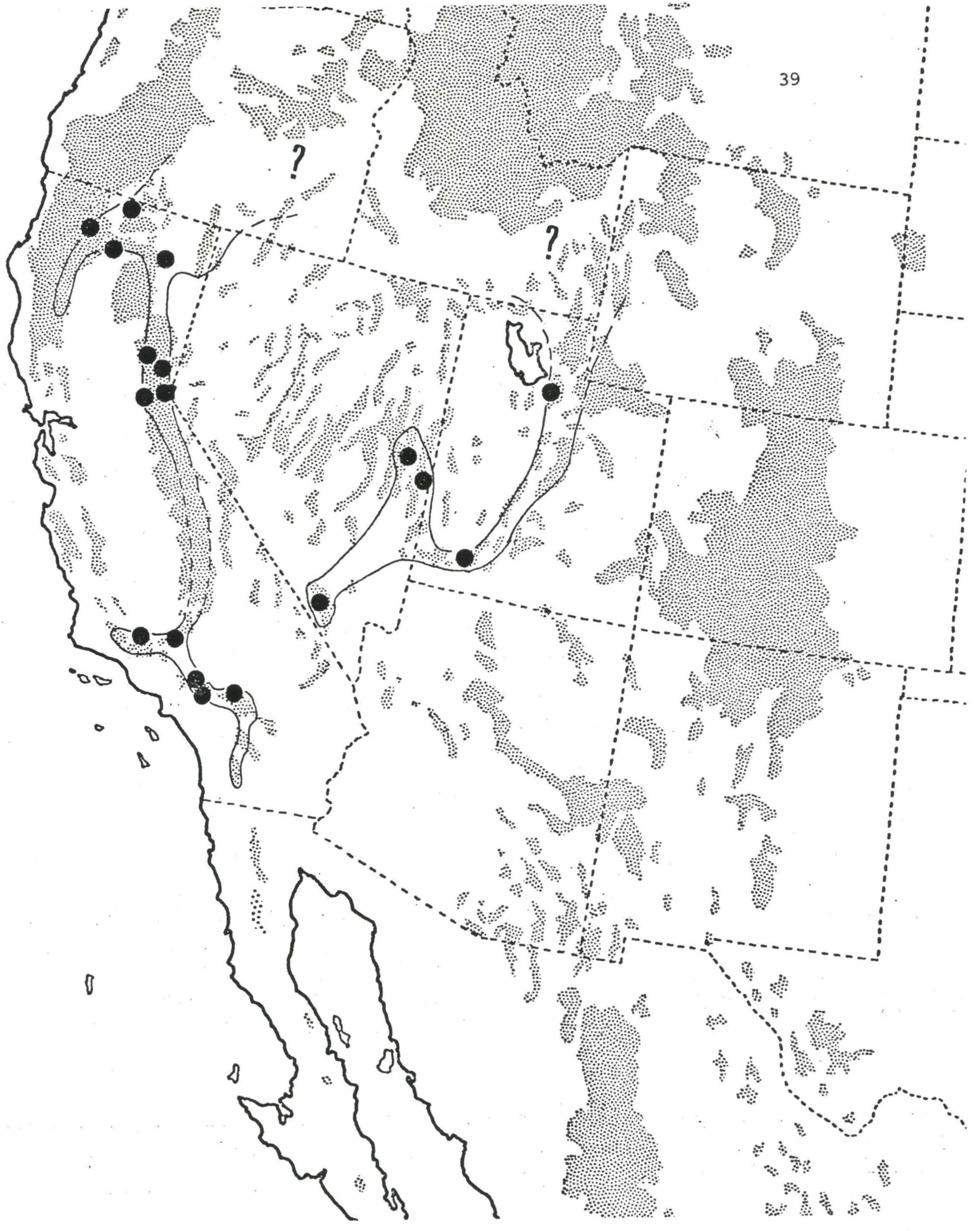
Fig. 2. Cumulative percent activity of Choristoneura retiniana and C. lambertiana subretiniana during 1974 at Ward Creek, 3 km S Tahoe City, Placer Co., CA, as indicated by nightly blacklight trap sampling. The mean in total numbers for both species was reached in the August 5 collection.



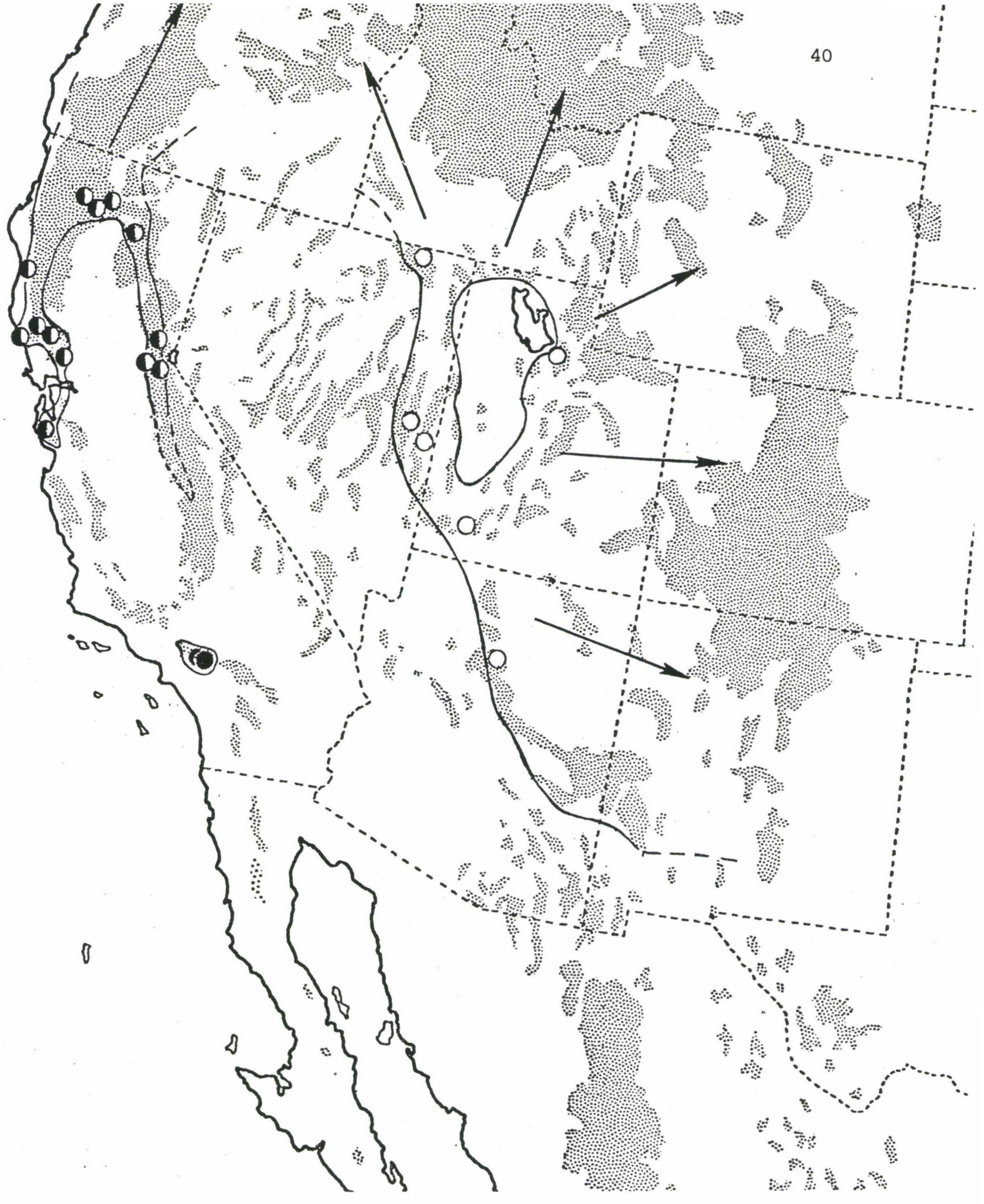
Map 1. Localities surveyed during 1978-1981, by larval collections, blacklight, and pheromone trapping.



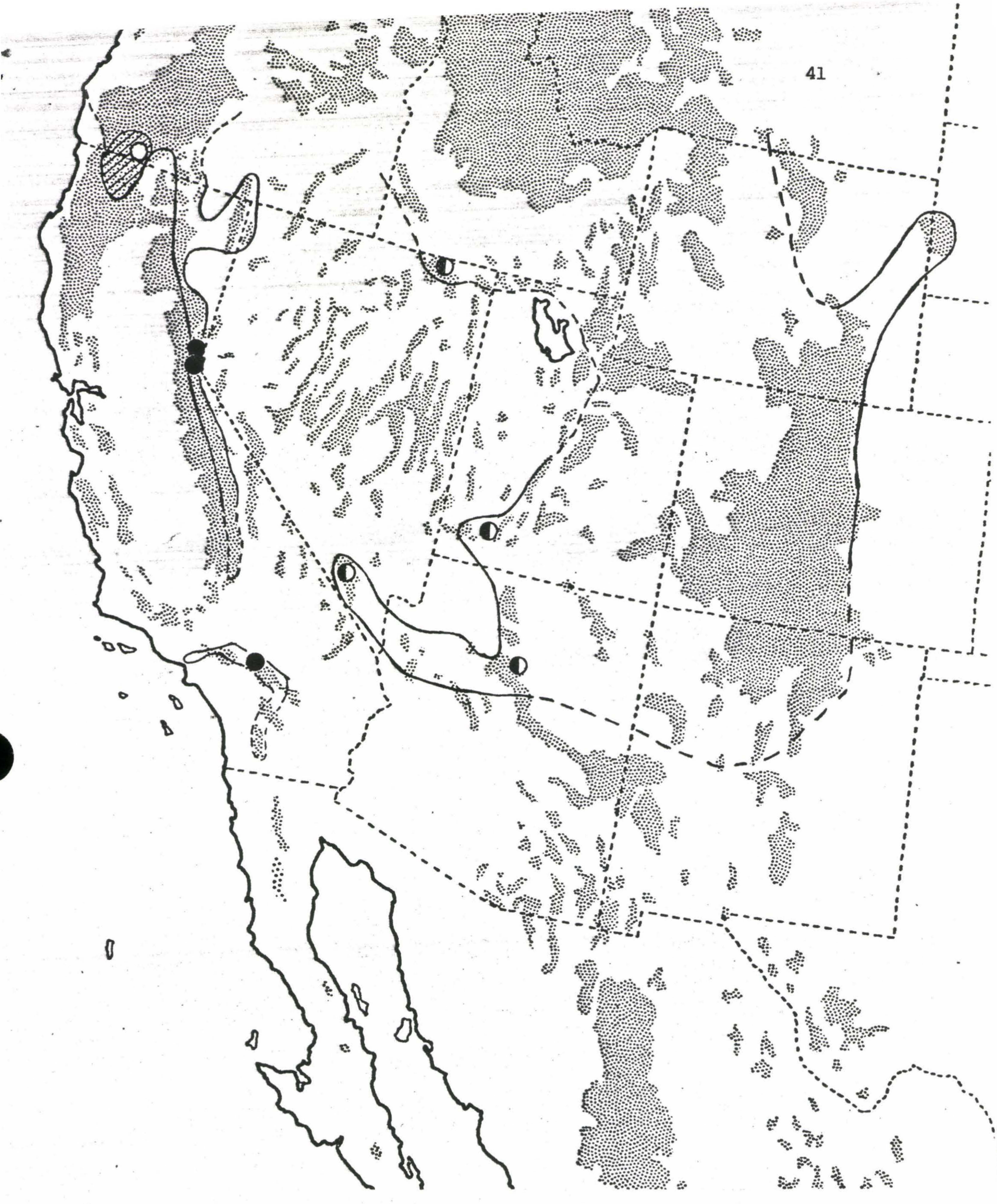
Map 2. Cross-population tests for attractiveness of virgin females
Open circles = Choristoneura retiniana, closed circles = C. carnana, half-closed circles designate sympatric associations at test sites.



Map 3. Geographical distribution of Choristoneura retiniana according to specimens examined. Symbols designate populations sampled during 1978-1981.



Map 4. Geographical distribution of the Choristoneura carnana - occidentalis complex in the southwestern U. S. Symbols designate populations sampled during 1978-1981: closed circles = C. carnana carnana; half-closed circles = C. carnana californica; open circles = C. occidentalis.



Map 5. Geographical distribution of the Choristoneura lambertiana complex in the southwestern U.S., according to specimens examined. Symbols designate populations sampled during 1979-1981: closed circles = C. lambertiana subretiniana; half closed circles = C. l. ponderosana. Open circle and cross-hatched area in California-Oregon indicates type locality and known range of C. l. lambertiana.